A conceptual framework for invasion in microbial communities

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Total number of authors:
12

Published in:
The I S M E Journal

Link to article, DOI:
10.1038/ismej.2016.75

Publication date:
2016

Document Version
Peer reviewed version

Title:

A conceptual framework for invasion in microbial communities

Short title:

Framework for microbial invasions

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Subject category:

Microbial ecology

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Introduction

Studies on invasion of microbial communities are gaining momentum, with a considerable increase in publications on invasion by pathogenic, beneficial, or commensal microbes. A better understanding of microbial invasion could generate significant payoffs across many domains including management of human and animal diseases, development of plant growth promoting inocula, and bioaugmentation in food and environmental industries. Experiments testing determinants of microbial invasion, such as resident community diversity and resource utilization, have been reported for diverse environments, including the gut of mice, the plant rhizosphere or wastewater treatment bioreactors (See Table S1). It is, however, challenging to draw broad conclusions from these studies as the used terminology lacks consensus, the experimental approaches are often inconsistent, and the observations are often anecdotal or even contradictory.

In plant and animal ecology, invasion has been an active research field for decades with controversies relating to its definition, boundaries, and specificities (Valéry *et al.*, 2008; Simberloff and Vitule 2014) . Controversies, such as the distinction between native and alien species and the necessity for an invasion to have a negative impact on the resident community, are not fully resolved. Nonetheless, efforts towards a unified framework for invasion biology have been made (Blackburn *et al.*, 2011). Similar controversies can affect the more recent field of microbial invasion – and the need to develop a general framework for microbial invasion, within which to synthesize individual observations, has been voiced before (Litchman 2010; Mallon, van Elsas, *et al*., 2015).

Here, we propose a simple definition of invasion in a microbial community (Table 1) as the *establishment* of an *alien microbial type* in this *resident community* and suggest a community ecology framework to interpret this process.

Defining and detecting invasion in microbial communities

What is an invader?

Consistent with our focus on invasion in individual microbial communities, we propose to follow the simple and inclusive definition of an invader commonly used in studies of plant or animal community invasibility, namely that any species (or- more generally- biological type) not currently part of the resident community can be considered a potential invader (Davis *et al.*, 2005; Tilman, 1997).

We recognize that other, more restrictive, definitions exists, especially when the focus goes beyond single communities and considers biogeography (i.e., when the key interest is whether or not species expand their biogeographical range). This is the case for the invasion biology framework presented by Blackburn *et al.*, (2011) where a potential invader should cross a significant geographical barrier. This non-nativeness implies the absence of recent ecological interactions with the resident organisms and, hence, the absence of prior co-evolution or co-adaptation. As a consequence, this type of alien organism is believed to have the potential to drastically modify the composition or functioning of the community it invades, although disagreement exists on this point (Davis *et al.*, 2011). In this framework the invader should also demonstrate its ability to successfully disperse from the initial invasion point to other communities (Blackburn *et al.*, 2011). A few reviews have adopted this invasion biology framework to examine microbial invasion (Litchman 2010; Amalfitano *et al.*, 2014), but noted that our incomplete knowledge of microbial biogeography makes it difficult to assess whether a microbial type has dispersed beyond its natural range. Other authors propose that a microbial type only qualifies as an invader if it enters “an environment or community where it has never before existed”(Mallon, van Elsas, *et al.*, 2015). This absolute, continuous, absence from the resident community is difficult to demonstrate for most communities. In summary, when the focus is on the

78 invasion of an individual community, and because there is no indication that aliens that have dispersed
79 out of their range are unique in their interactions with a resident community, we suggest accepting
80 any types not currently present in the resident community as potential invaders.

81 *Resident community*

82 We define the resident community simply as any given community investigated for potential invasion.
83 This definition is on purpose very general as it makes no assumption regarding community properties
84 such as the existence of a temporally stable 'core' group of microbial types, of stable functional
85 attributes, or of a long common history (e.g., it includes synthetic communities assembled shortly prior
86 to invasion De Roy *et al*., 2013; Mallon, Poly, *et al.*, 2015). This choice implies that invasion is not
87 restricted to stable, closely monitored communities. However, some knowledge of the composition of
88 the resident community is needed to establish the alien status of the invader. Cataloging all microbial
89 types to a specific genotype can be challenging for many microbial communities, which are often
90 immensely diverse. Therefore, the resident community can simply be defined *a minima* as a
91 community that, prior to invasion, did not contain the invader (e.g., De Roy *et al.*, 2013; van Elsas *et*
92 *al.*, 2012). Establishing the absence of the invading type prior to invasion requires either expert
93 knowledge of the microbial system considered or sensitive detection methods targeting the alien type
94 directly (via growth-based, molecular, or microscopic methods) or targeting a trait or function unique
95 to the alien type. We acknowledge that absolute proof of absence is often impossible to provide
96 outside of the specific case of synthetic communities, but demonstrating that the alien type was below
97 the limit of detection of an appropriately sensitive method is generally accepted in practice (Acosta *et*
98 *al.,* 2015).

99 The fact that many microbes can remain dormant for long periods (Lennon and Jones, 2011) may
100 justify a more restrictive definition of a resident community. Indeed, due to their reduced metabolic
101 state, these microbes could be considered to have too little ecological interactions to truly be part of
102 the community. A dormant microbial type would then be regarded as alien upon reactivation, an entry
103 route to the resident community not traditionally considered. If such an activity-based definition has
104 merits, it also complicates the census of the resident community.

105 Defining the spatial limits of a community can constitute an arduous challenge (Konopka, 2009). While
106 it is trivial for laboratory studies (e.g., a microtiter well) or for certain systems that are clearly limited
107 (e.g., the oral cavity of a patient), other systems (e.g., in soil, river) have no obvious boundaries. On the
108 one hand, the microbial composition of these natural systems does not seem to present
109 discontinuities as exemplified, for soils, by the progressive decrease with distance of the genetic
110 similarity of the members of a free living bacterial species (Vos and Velicer, 2008). On the other hand,
111 significant variations of antibiotic inhibitory interactions among Streptomycete communities on $1m^2$
112 have been observed, that suggest distinct selective environments among these locations (Davelos *et*
113 *al.*, 2004). In this case, community boundaries could be defined through similar antibiotic inhibition
114 abilities. Diffuse boundaries obviously challenge the applicability of the concept of community invasion
115 in many natural ecosystems as it does for other community ecology concepts (Konopka, 2009), but
116 attempts to define spatial limits of a resident community can be made even in highly complex natural
117 systems.

118 *Establishment*

119 While the first event in community invasion – the entry of the alien microbial type – is self-
120 explanatory, defining and accurately measuring the next step – establishment – is more difficult. In

general ecology, establishment is defined as the persistence of the alien type as a self-sustaining population in the new environment, due to exploitation of its resources (Davis *et al.*, 2005). For many microbes, a single cell theoretically suffices to develop a population, but we propose the maintenance of a metabolically active population of invaders for a significant period of time, as a better operative criterion. Qualifying further the 'significant' period of time needs to be based on the characteristics of the resident community because communities can differ dramatically in biomass turnover rate and temporal variability. A time horizon for establishment can be based on the average renewal time (T_R) of the biomass in the community. This can be calculated as T_R = N / (Y * F_S); where *N* (biomass) is the amount of biomass of the resident community, F_S the flux of substrate to the community (mass of substrate per unit time), and Y, the 'effective' yield of the community (biomass per mass substrate). We suggest monitoring the community over a few T_R before concluding on the alien's establishment. It is also relevant to include several iterations of any known cycles the habitat is exposed to (e.g., seasonal cycles for natural communities, operational cycles for engineered systems) before deeming the invasion successful. Ensuring that the alien maintains an active population may be warranted if suspicion exists that the alien might only persist in dormant form (e.g., spores) or even as nucleic acid remains which could still be detectable by PCR, for example. This demonstration is not required if the population dynamics of the alien indicates local growth, for example by reaching larger abundance than upon entry (increase from rarity), an unlikely occurrence in many invasion experiments where the alien type is introduced at very high abundance.

Invasion consequences

A debated criterion in defining invasion pertains to its consequences. In accordance with Blackburn *et al.*, (2011), we propose omitting the requirement that the establishment of the invader negatively impacts the community. This omission is controversial due to the negative connotation of the word

144 'invasion', but we argue that 'negative impact' is a vague criterion. Indeed, 'impact' can be measured
145 in multiple ways on myriads of different community attributes (abundance of resident populations,
146 community richness, community functional attributes, etc.) that may not directly relate to the invader,
147 because the establishment of an invader can have both positive and negative consequences on
148 different community members (Valéry *et al.,* 2008).

149 *Invasion experiments in the view of the proposed definitions*

150 While there are many applied studies that may be relevant to the framework presented here,
151 including biofilm colonization, bioaugmentation, and competition studies, we focused our evaluation
152 of the literature on studies specifically using the term "invasion" (Table S1). These studies, however,
153 do not use explicit definitions or measurement criteria. For example, the concept of a resident
154 community is often approached loosely, particularly when synthetic assembled communities are
155 added together with the 'invader'. In these cases, nothing, from an ecological perspective,
156 distinguishes the 'resident' community members from the 'invader' since none have had a prior
157 common existence. In many studies, proper controls proving the absence of the invader from the
158 resident community are either missing or not reported. Finally, many studies declare successful
159 establishment when persistence is assessed over a short, unjustified time period.

160 **Microbial invasion in a community ecology perspective**

161 We can categorize the invasion literature into two classes depending on whether the focus is on the
162 invader, or on the resident community. Invader-centric research focuses on the invader's traits
163 (Hambright *et al.,* 2014) and, for example, compares the invasiveness of different alien types (Ma *et*
164 *al.,* 2015). The largest share of the literature, however, is 'resident community centric' and thus
165 evaluates community invasibility (Table S1). Often, the authors create an array of communities with

166 variation in an attribute (e.g., richness, evenness, genomic dissimilarity) by manipulating natural
167 communities (e.g. decreasing diversity via dilutions and stress perturbations) or by assembling
168 synthetic communities and evaluate the importance of that attribute in invasibility. Synthetic
169 communities, assemblages of a limited number of pure strains (De Roy *et al.*, 2013) sometimes all
170 belonging to the same species (Hodgson *et al.*, 2002; Eisenhauer *et al.,* 2013), are very attractive
171 because they afford great control on experimental design (De Roy *et al.,* 2014). However, it is unknown
172 to what extent these communities are suitable models for natural communities where more complex
173 ecological interactions likely exist. Thus, the success of invasion in synthetic communities might
174 depend on different factors compared to natural communities, where a longer history of ecological
175 interactions has shaped community composition.

176 The reviewed studies on invasion do not adhere to a systematic ecological framework. In most
177 experimental studies that have a community ecology emphasis, the focus is on competition for
178 electron donors and/or acceptors as well as micronutrients. However, this common focus is sometimes
179 obscured by the use of a variety of terms across papers (e.g., niche overlap, niche dimensionality,
180 resource utilization). We propose that adopting the framework of community ecology developed by
181 Vellend, (2010) can help clarify the potential determinants of invasion. This framework identifies four
182 fundamental processes that control community dynamics: (1) selection, (2) drift, (3) diversification and
183 (4) dispersal.

184 Dispersal includes both immigration and emigration. An alien type will have more opportunities to
185 immigrate into a community when dispersal to the resident community is strong. Dispersal is not
186 considered in the majority of microbial invasion studies conducted in closed batch systems (Table S1),
187 but may be critical to invasion success. The dispersal rate, defined as the number of entering cells per
188 unit of time, largely depends on the environment. Lindström and Langenheder (2012) reviewed

189 regional factors that can influence dispersal rate in a given environment. They suggest that dispersal
190 limitation plays a bigger role in terrestrial environments compared to aquatic environments. As
191 dispersal is mainly passive for bacteria, at least on macroscopic spatial scales (for example dispersal via
192 air, aerosols or with water flow in soil environment), it can be modeled using mechanistic aerodynamic
193 and hydrodynamic models similar to those used for plant seed and zooplankton dispersal (Michels *et*
194 *al.*, 2001; Kuparinen *et al.*, 2007). The abundance of an alien type population entering the resident
195 community can be quantified as the product of its dispersal rate by the duration of dispersal. If this
196 abundance is low, the probability of establishment can be reduced (Blackburn *et al.,* 2015) because a
197 few immigrants are more subject to stochastic events that may lead to their extinction. This assertion
198 has been confirmed for macro-organisms, but is rarely addressed for microbial communities, although
199 a recent study on algal invasion provides supportive evidence that the quantity of invader is key
200 determinant of invasion success (Acosta *et al.,* 2015). In fact, in most of the literature we reviewed, the
201 alien type is added in high numbers, during a single immigration event (Table S1).

202 After alien entry, selection and/or drift are the main processes determining its establishment.
203 Selection pressure on the invader can be positive or negative depending on the resident community's
204 composition, its dynamics, and the environmental conditions. This can be conceptualized by
205 considering the potential niche overlap between the alien type and the resident community. In
206 extreme cases, the alien can fill an empty niche because it possesses metabolic traits absent from the
207 community (transiently or long-term) and can thus easily establish (the case of bioagumentation).
208 More commonly, the alien type is required to out-compete at least one member of the resident
209 community in order to establish itself. This can occur if the alien possesses traits that allow it to
210 displace a resident from the same niche. The role of selection- and specifically of competition for
211 resources- as a determinant of invasion has been the subject of several studies on microbial

212 community invasion (Table S1). Richness (and/or genomic dissimilarity) of the resident community is
213 often used as a proxy for its ability to compete with the alien type (Dunstan and Johnson 2006; Jousset
214 *et al.*, 2011), because more diverse communities have higher probability to host resident types that
215 are competitively superior to the alien either as individuals or as interacting types (Figure 1A). This
216 assumption is sometimes supported experimentally by measuring the resource utilization pattern or
217 the productivity of the resident communities (as a whole or as individual members) and of the alien
218 type (e.g., Hodgson *et al.*, 2002). Indeed, more diverse resident communities are usually less prone to
219 the establishment of an invader. In a similar vein, invasion success increases with phylogenetic
220 distance between the alien and the resident species in synthetic communities of a few bacterial strains
221 (Jiang *et al.*, 2010). The importance of the resident community composition implies that the timing of
222 the alien entry relative to the prior history of the resident community may also be determinant in the
223 invasion success. Communities that have had less time to assemble are likely to contain fewer types
224 with broader niches and lower competitive abilities than communities that have 'matured' longer
225 (Shea and Chesson, 2002). Invasion success would then be higher in less mature communities.

226 Selection in a community can be markedly affected when the community is subjected to ecological
227 disturbance (Shade *et al.*, 2012; Ma *et al.*, 2015). Disturbances tend to decrease community density
228 and diversity, potentially increasing the available niche space – in other words temporarily decreasing
229 competition. The invader establishment then depends on its ability to cover the available niche space
230 of the disturbed community (Liu *et al.,* 2012; De Roy *et al.,* 2013).

231 Neutral drift refers to a process where community structure changes stochastically through
232 demographic processes of 'birth' (or division) and death. If all community members have equal fitness,
233 then drift is important: the establishment of the alien type is then random, depending mainly on its
234 relative and absolute abundance (Figure 1B). Under pure drift, the long-term probability of invader

disappearance is one minus its initial frequency, and the rate of disappearance is negatively related to community size (Vellend, 2010). Although it cannot be easily quantified, drift is always present in biological communities but this process is especially important in communities of low abundance, because discrete division/death events have stronger consequences. Therefore, a disturbance that durably decreases the size of the community would increase the role of drift.

Current invasion research focuses predominantly on the correlation between invasion success and resident community diversity. If these studies have contributed to our understanding of how communities dominated by selection are responding to invasion, we emphasize that further considerations are necessary. The dynamics of microbial communities are usually governed by more than one process and, as we indicated above, in communities where drift is stronger than selection, resident community diversity will not play a critical role in invasion success. Instead, the initial relative and absolute abundance of the invader should be a key determinant of establishment (Figure 1).

Lastly, communities can increase their diversity through the acquisition of new genotypes that emerge from ancestral genotypes due to diversification. Diversification can occur in the invader population or in the resident community and is thought to be positively related to population size. Some bacteria can diversify rapidly (within a few days) when introduced at high abundance in a habitat, even in presence of a resident community (Gómez and Buckling, 2013). diversification can increase the chances for an alien type to establish if some of the mutations are adaptive (Tayeh *et al.,* 2015). Conversely, diversification of the resident community members might produce insurance effects and increase community resistance to invasion.

Recommendation for future research

We proposed a definition of invasion where every microbial type not present at a particular time in a community is a potential invader. This is appealing because this framework is consistent with accepted ecological research terminology and is easily and coherently applicable to any microbial community. It not only clearly highlights the fundamental ecological similarity between seemingly disparate concepts such as bioaugmentation, pathogen suppressive communities, or microbiome enhancement, but it also indicates that community invasion should be considered as a 'normal' event in community assembly and is commonplace in most communities. However, more restrictive definitions might be needed once we know more about the stability of microbial communities. For example such future definitions may exclude conditionally rare types from the scope of invasion because of their frequent transient occurrence within communities. Additionally, the resident community may need to be defined more clearly as a community with historical interactions among its members and with its environment.

By presenting invasion research in a community ecology framework, it is apparent that some processes have received more attention than others. A selection focus has overwhelmed invasion research, while other processes shaping community dynamics are rarely considered. For example, in batch experiments with sterile feeds, dispersal in the community is often completely interrupted, except from the introduction of the alien type. Therefore, the impact of the dynamics of the resident community on invasion is neglected. Similarly, the absence or the constant supply of nutrients to the community during an invasion experiment might not simulate the native conditions of the community correctly. In fact, when nutrients are supplied in a dynamic fashion, the outcome of the invasion can change (Liu *et al.,* 2012; Mallon, Poly, *et al.,* 2015). Overall, we suggest designing experiments focusing on the role of dispersal, drift, and diversification, because these processes have received less attention. In this way, a complete picture of invasion as a community process can be obtained

The discussed community ecological framework, combined with appropriate experimental conditions and measures of invasion, can be used to posit and test hypotheses on invasion that consider alien type and resident community in one coherent framework. We emphasize that invasion should be considered as a part of 'normal' community assembly and not only seen as something with negative consequences. The applications of such framework range from controlling environmental processes like water treatment to human microbiome improvement. We believe that such efforts will progress the study of microbial invasion.

Acknowledgement

This perspective is the outcome of discourses during the cross-institutional projects MERMAID (An Initial Training Network funded by the People Programme - Marie Skłodowska-Curie Actions- of the European Union's Seventh Framework Programme FP7/2007-2013/ under REA grant agreement n°607492) and the Inter-University Attraction Pole (IUAP) project µ-manager funded by the Belgian Science Policy (BELSPO, P7/25). The authors also acknowledge support from the King Abdullah University of Science and Technology.

Supplementary information is available at The ISME Journal's website

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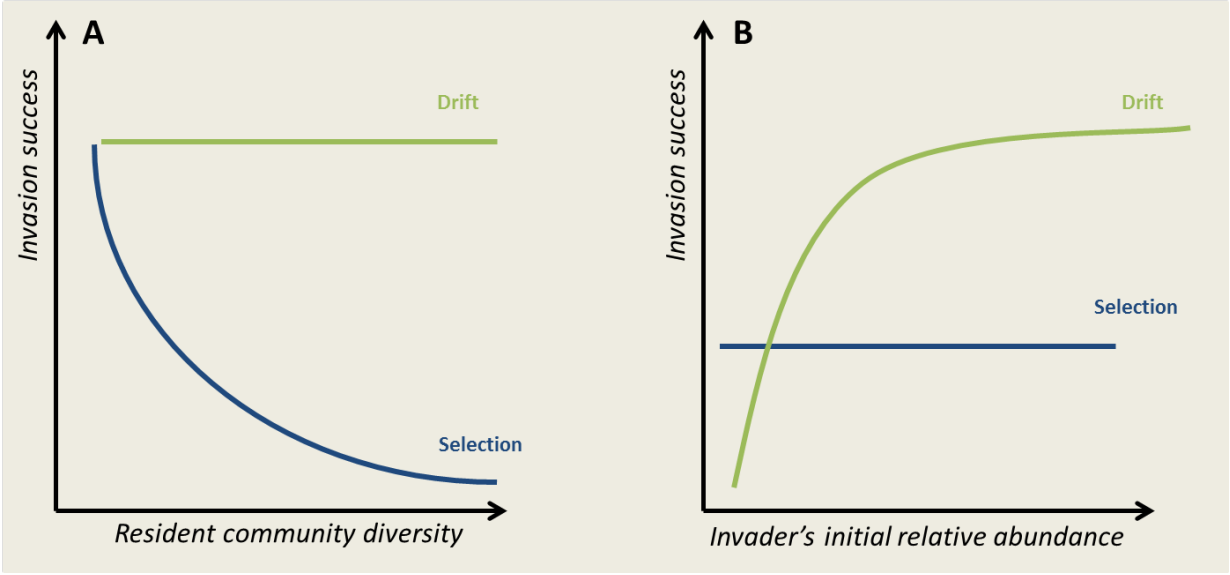

Figure 1. Hypothetical relation between average invasion success and (A) resident community diversity and (B) initial relative abundance of the invader, in communities where either competition (selection) or drift govern community assembly. In panel A, the exponential curve is illustrative; the curve can be of any monotonic form, with the rate of decline depending on the distribution of the competitive abilities of the resident microbes relative to that of the alien. In panel B, the curve associated with drift highlights the fact that, in a drift only situation, invasion success increases rapidly with the size of the invading population. For example, simulating drift with the *untb* package (Hankin, 2007) shows that if an alien enters at 1% relative abundance or more in a community with a death and birth rates of 5% per generation, invasion success (persistence of at least one alien cell) after 5 biomass turnover time is almost certain.

386 Table 1. Terminology and Definitions

Term	Definition	Reference
Microbial community	Group of potentially interacting microbial types that co-occur in space and time	Nemergut *et al.*, 2013
Resident community	A specific community considered in the context of possible invasion	This study
Alien type or invader	A microbial type that was not part of the resident community prior to point of observation	Adapted from Davis *et al.*, 2005
Community assembly	The sum of all processes that shape the composition of a microbial community, including dispersal, selection, drift and diversification	Adapted from Vellend, 2010
Dispersal	Movement of organisms across space, considering immigration in and emigration out of a community	”
Selection	Changes in community composition caused by deterministic fitness differences between types	”
Drift	Changes in the relative abundance of types in a community over time caused by stochastic processes	”
Diversification	Increase in diversity of types in a community caused by generation of new genetic variants	”
Invasion	Entry and establishment of an alien type in a resident community	Adapted from Blackburn *et al.*, 2011
Establishment	The maintenance of an active population of an alien type in a resident community for a significant period of time	This study

387